Comparative Anatomy of the Digestive System of Rural and Urban Raccoons (*Procyon lotor*) in Central Ohio

Research Thesis

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By

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ABSTRACT

Since the industrial revolution, urban landscapes are ever expanding. This urbanization impacts the surrounding flora and fauna. As the landscape changes, the ecology changes with it. Animals must acclimate to new restrictions and novel diets. Some animals are adept at exploiting these resources and others are forced to colonize adjacent habitat. Raccoons (*Procyon lotor*) are an iconic urban dwelling animal. This adaptive creature inhabits most of North America and occupies every level of urbanization from forested areas to city centers. It feeds on a variety of foods from seeds and nuts to small mammals. A raccoon's wide diet is critical for its successful acclimation to many environments. Remarkably, very little research has been done on the digestive system of this animal. I will be the first to document the macro-anatomy of the gastrointestinal (GI) tract, and to consider its implications for adaptation to environment. The GI tract starts with teeth that were examined for changes in omnivory using the fourth premolar and the first molar sheering and crushing ratios. I found little evidence of change across ecologies indicating physical changes. The hollow organs, of the stomach, small intestine, and large intestine were analyzed for significant differences in surface area to volume ratio and for length and weight differences. These aspects of the GI varied widely across ecologies and individuals indicating that the general size and shape does not change based on diet. Of the hollow organs the esophagus differed in normalized circumference across environments and suggests gorging capabilities may differ between ecologies. The solid organs of digestion, liver (with gallbladder), greater omentum and the pancreas were normalized and evaluated for weight similarly to the hollow organs. The evaluation of the relative size of these organs did not differ between habitats. It is difficult to say with confidence that there is a significant difference in the gut morphology between rural and urban raccoons. This study provides an in-depth investigation of the gut

anatomy of *Procyon lotor* and a fundamental basis for exploring the effects of human expansion on indigenous fauna. The future holds more studies, with increased specimen numbers including histology and DNA profiles.

Acknowledgments

I would like to thank Dr. Jonathan Calede for taking on this project with faith that I could succeed. I would also like to include Dr. Jackie Augustine for volunteering her time to grow the next generation of scientific inquiry; Dr. John Maharry for supporting new ideas and students with the Dean's Undergraduate Research Scholarship and Mr. Ed Quinn for his efforts and flexibility in making this project a reality. This study would not have been as possible without the help of Jared Miller, wildlife manager for Varment Guard Wildlife Services his tremendous respect for life compelled him to donate raccoons and reduce needless waste. I would also like to acknowledge the EEOB department of The Ohio State University for opening doors to studies like this on the Marion Campus. Part of this research was funded by startup funds from The Ohio State University. Finally, I thank Rileigh and Elliot Roscoe for assisting in specimen collection, data analysis, and editing.

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Field of Study

Biology Pre-Health Focus

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INTRODUCTION

The term synurbanization coined by Andrzejewski et al. (1978) refers to the adaptation of wildlife to urban environments. Urban landscapes have increased by 24% since 1980 across the United States (Alig, Kline, & Lichtenstein, 2004). On an evolutionary timeline, the urban environment is an explosive novel habitat (Luniak, 2004) and human induced changes to landscapes are one of the biggest influences on ecological change as a whole (Oro, Genovart, Tavecchia, Fowler, & Martínez-Abraín, 2013). Land development creates ecological changes in food and shelter availability. Artificial boundaries like roadways fences and high foot traffic areas block off avenues of dispersion and create denser populations of animals forced to live together (Dickman and Doncaster, 1987). The natural range of the raccoon averages to 122 acres while in urban environments it varies depending on influential structures (Dickman and Doncaster, 1987). Human presence changes ecosystems by interfering with predator-prey interactions, forcing cohabitation of incompatible urban animals, and increasing community density (Bateman & Fleming, 2012).

Some marked changes seen in urban environments are given as examples. The diurnal patterns of humans drive urban mammals to be more nocturnal (Gaynor, Hojnowski, Carter, & Brashares, 2018). The increase in anthropogenic food sources leads urban animals in having more offspring and more breeding cycles than their rural counterparts due to increased availability of food (Ditchkoff, Saalfeld, & Gibson, 2006). The increased breeding success drives an increase in density causing closer proximity of urban wildlife, facilitating the spread of disease (Ditchkoff et al., 2006). In adjacent studies, successful exploitation of urban food sources can negatively affect a birds brain development due to lack of antioxidants in their food sources (Møller & Erritzøe,

2015). The untoward effects of human expansion alter social, physical, behavioral, survival and nutritional aspects of urban mammals (Ditchkoff, Saalfeld, & Gibson, 2006; Bateman & Fleming, 2012).

These human induced stressors and anthropogenic foods have been known to cause microevolution. The color patterns of peppered moths changed to meet the color scheme of industrialized areas. Morphological changes in beak sizes and leg length of the house sparrow can occur in as little as 50 years due to differences in urban environments (Johnston & Selanders, 1964; Oro et al., 2013). Following the closing of dumps in Yellowstone Park, male grizzly bears (*Ursus horribilis*) fluctuated in size and symmetry of their canines, a trait known to be under sexual selection along with body size. The fluctuation is suggested to be a result of anthropogenic foods and a lack of sexual selection on that trait. These anatomical changes occurred rapidly in large, well-fed bears and were in conjunction with human activity. (Badyaev, 1998).

Because one of the major ecological changes due to urbanization is diet, I will focus on the gastrointestinal (GI) tract and associated solid organs (Oro et al., 2013). The goal of my research is to accumulate data on individual raccoons from rural and urban areas in central Ohio and compare data to determine if there is anatomical change due to a novel ecology. I purpose to investigate the role of urbanization on an iconic North American mammal still present in its native rural environment and in anthropogenically altered habitats: the common raccoon, *Procyon lotor*. This animal is common in urban centers where it has lived since the 1920's (Ulf, 2001); there, it feeds on anthropogenic foods (Bateman & Fleming, 2012). Raccoons do not

hibernate; they are a generalist and a solitary animal that can tolerate proximity to other common urban inhabitants (Lotze & Anderson, 1979). Raccoons in rural areas are opportunistic; they feed on the berries, nuts, and seeds of various plants (includes grains in small amounts), arthropods, and carrion in varying proportion, depending on seasonal availability. Raccoons prey on small vertebrates and larger vertebrates if the prey is wounded or trapped (Lotze & Anderson, 1979). In urban environments, raccoons exploit terrestrial food sources including landfills, restaurant wastes, individual trash bins, roadkill, and bird feeders. Their primary food source is plant matter and invertebrates as availability dictates; however, they frequently supplement with anthropogenic refuse, small mammals (rats and rabbits) and food sources like bird feeders and pet food. The supplementation is more common in the winter months (Oro et al., 2013; Rulison, Luiselli, & Burke, 2013). In urban environments, raccoons frequently ingest non-food items (e.g., plastic, rubber bands, cigarette butts etc.) that can be found in their feces (Hoffmann & Gottschang, 1977). These differences in ecology are well documented as are behavior patterns in *P. lotor.*

The peritoneal cavity of *P. lotor* has not been extensively studied, photographed or documented. Related studies include lactation in conjunction with digestive organ size, retention time studies and broader studies that cross multiple taxa but do not focus on specifically raccoons (Derting, 1996; Elston & Hewitt, 2016; Luniac, 2004; MacDonald & Pickett, 1990). The gastrointestinal capabilities based on objective data is a novel idea for exploring questions of adaptation to anthropogenic forces. I hypothesize that I will see morphological differences in the GI tract of the raccoon due to feeding on temporo-spatially predictable food sources in urban populations that differ from their naturally occurring, rural, diet. The spur winged goose has an alimentary

canal that varies based on their diets; fiber content location and time of year play a factor. Larger fiber content is correlated with larger digestive organs to include liver and hollow gut (Halse, 1985). I set out to explore if similar changes occur in raccoons given an abrupt change in ecology. I expect to find a longer intestine, both small and large, in urban raccoons to facilitate longer retention time for fermentation of their preferred fiber. A large stomach and esophagus will allow for expedited gorging in the urban raccoons, given their feeding frequency is not necessarily seasonal (Prange et al., 2016) I also predict that the solid digestive organs of urban raccoons will be larger in comparison to their body mass due to increased need to filter out toxins and process more refined sugars and fats common to their urban diet (Rulison et al., 2013). The gallbladder will also have more volume in the urban raccoon to digest fats common to anthropogenic food sources (Kaneko et al., 2009). In the context of macro-anatomy, I predict that the rural raccoon will have a larger surface area to volume ratio because they are adept at digesting their natural diet and extracting all available nutrients in scarce amounts of food where the urban raccoon does not experience scarcity as frequently (Andrzejewski et al., 1978).

MATERIALS AND METHODS

I documented the gross anatomy of the digestive system of eight specimens of the common raccoon (*Procyon lotor*). I dissected five specimens from a major American urban center, Columbus, Ohio. I also dissected three raccoons from rural counties of central Ohio. The US Census Bureau's designation system was used to differentiate rural and urban raccoons (United States Census Bureau, 2011). All animals were salvaged under Ohio Department of Natural Resources wild animal permit 20-229 or donated by hunters and pest control companies. They were all collected during the months of January and February of 2019, except for one specimen collected in November 2018. All specimens were frozen until study (Table 1).

Table 1. Specimen information for raccoons dissected for this study.

Specimen	GPS Lat	GPS Long	DNA Sample #	Date of Death
RMH1	40.5238629 N	82.7574003 W	PR19-PL1	1/6/2019
RMH2	40.5238629 N	82.7574001 W	PR19-PL2	1/7/2019
RMS3	40.5712130 N	83.0852530 W	PR19-PL3	11/2/2018
UFE1	40.0713660 N	83.0174645 W	PR19-PL4	1/22/2019
UFE2	40.0930643 N	83.0115678 W	PR19-PL5	1/21/2019
UME3	40.0930643 N	83.0115678 W	PR19-PL6	1/21/2019
UFE4	40.0752610 N	83.0024070 W	PR19-PL7	2/15/2019
UME5	40.0699560 N	83.0762710 W	PR19-PL8	2/13/2019

All specimens were washed, and towel dried after thawing. I measured the body mass of individuals using a spring scale (± 10 g) and measured its snout-to-vent length and circumference (at the widest point of the abdomen) using a tape measure (± 1 mm). I then measured the skull length (Table 2). These data were used to normalize measurements taken throughout the study. Age was determined by baculum size and uterus scars, these aspects determine sexual maturity (

Table 2. Body measurements of the specimens included in this study. Body mass in grams; skull length, snout-to-vent length, and body circumference in centimeters. Body circumference is measured at the widest point on the abdomen.

Specimen	Body mass	Skull length	Snout-to-vent length	Body circumference
RMH1	4,600	11.1	58.2	37.5
RMH2	5,700	10.8	57.8	43.2
RMS3	7,100	12.0	65.5	50.0
UFE1	6,100	10.5	62.1	42.5
UFE2	5,300	10.5	59.5	39.7
UME3	2,900	10.0	51.1	40.9
UFE4	4,500	9.8	53.4	39.9
UME5	6,400	10.7	56.5	48.2

I measured the upper fourth premolar and first molar using Mitutoyo digital calipers (± .01mm). The teeth were measured following the approach of Popowics (2003) used by Calede et al. (2018) (Fig. 1). The measurements taken are correlated with diet, and in particular the degree of omnivory in small carnivores (Mephitidae, Mustelidae, and Procyonidae) (Popowics, 2003; Calede et al., 2018). Each animal was sexed and females were expressed to test for lactation. Lactation correlates with the weight of the gastro-intestinal tract and could affect the results of this study (Derting, 1996).

The thoracic and peritoneal cavities of all specimens were opened from the angular process of the mandible to a point located two centimeters anterior to the anus (Fig. 2). First, the greater omentum was carefully dissected from the greater curvature of the stomach. The junction between the small intestine and the large intestine was identified by a thickening of the bowel tissue (Fig. 3) on the undisturbed gut tube, prior to any other dissection (Setvens and Hume, 2004). I removed both the gut tube (esophagus, stomach, small intestine, and large intestine) as well as the abdominal accessory digestive organs (liver and pancreas) from the body cavities. I also extracted the spleen for the purpose of DNA sampling. In all specimens,

Figure 1. A photograph of P3, P4 and M1 (top to bottom) of RMH1 (Left); The corresponding measurements taken of P4 and M1 (right). Abbreviations: **P4LB**, length of P4; **P4W**, width of P4; **P4PM**, length of basin on P4; **PRBL**, length of shearing blade on P4; **M1BL**, length of shearing surface on M1; **M1LL**, length of M1; **M1W**, width of M1.

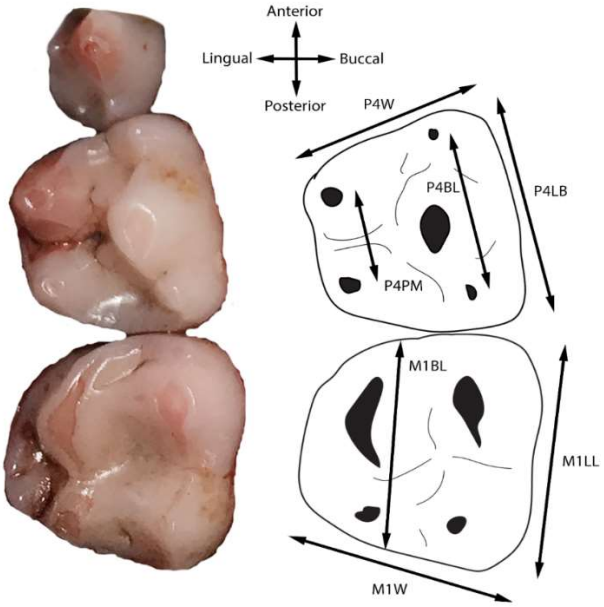
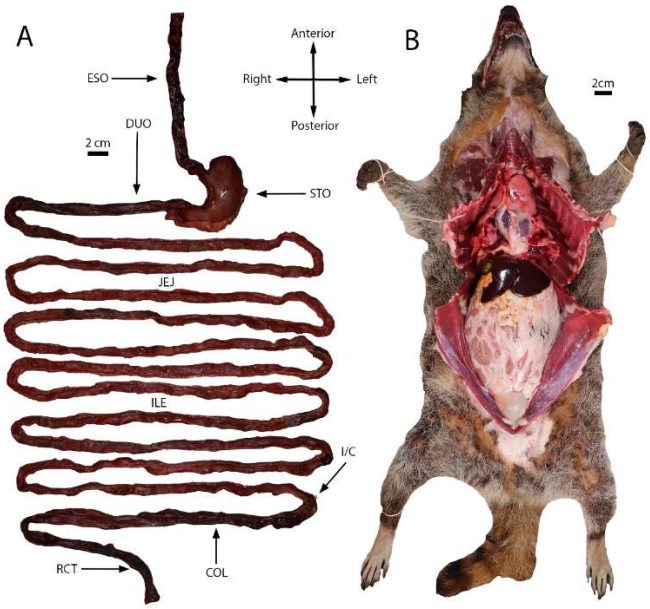
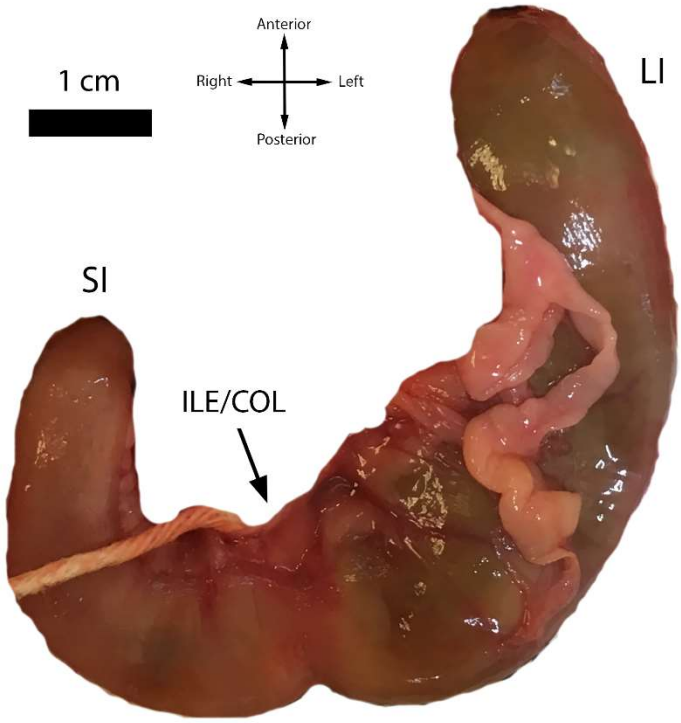


Figure 2. A, Photograph of the gastrointestinal tract of *Procyon lotor* with arrows pointing to individual segments of the alimentary canal; B, the ventral view of *Procyon lotor* after opening the ventral abdominal wall. Photograph of the in-situ position of the abdominal cavity, the greater omentum obscures the view the intestines and the liver obscures the view of the stomach. Abbreviations: **ESO**, esophagus; **STO**, stomach; **DUO**, duodenum; **JEJ** jejunum; **ILE**, ileum; **I/C**, ileocolic junction; **COL**, colon; **RCT**, rectum.



I severed the esophagus at the junction with the glottis and the large intestine at the anal sphincter. I weighed the liver, pancreas, and empty gallbladder (Fig. 4). I measured the volume of the gallbladder by filling it with water using a graduated gravity pipet (± 1 ml). I measured the length of the entire gut tube (Fig. 2) as well as the individual lengths of the esophagus, small intestine, and large intestine with a tape measurer (± 1 mm) on a wet work bench to minimize stretching. Each portion of the gut tube was also weighed using a Cen-tech digital scale (± 1 g). I measured the length of the stomach from the fundus to the pylorus and its width perpendicular to the midpoint of the lesser curvature using a tape measure (± 1 mm). I butterflied the stomach by cutting it along the greater curvature from pylorus to esophagus (Fig.5). The stomach contents were removed and analyzed for parasites using a strainer. I used ImageJ (Schneider, Rasband & Eliceiri, 2012) to calculate the surface area of the butterflied stomach. I also weighed the stomach. Each specimen studied was sampled for DNA by taking samples from the liver, kidney, and spleen; samples are reposited at The Ohio State University Museum of Biological Diversity. I calculated the surface area of each of the organs of the gut tube using their length and their mean radius; the radius was determined from the circumferences of the distal and proximal end of each organ, it was measured from a two-centimeter section of the organ cut longitudinally. The esophagus does not take part in absorption of nutrients so it was measured for its mean circumference from anterior and posterior measurements. The lengths of the hollow organs were then normalized by skull length, a more reliable proxy for body size than snout-to-vent length (Van Valkenburgh, 1990) (Table 3). This enables the study of the relative proportions of the digestive organs, irrespective of absolute individual size. The masses of the pancreas, liver, stomach, whole gastrointestinal tract, and greater omentum were normalized by body mass (Table 4).

Figure 3. A photograph of the ileocolic junction (ILE/COL) in-situ. The junction, indicated by an arrow, connects the small intestine (SI) to the large intestine (LI).



The mean esophageal circumference was normalized by skull length. To determine surface area to volume ratio, I first calculated the truncated cone volume using the posterior and anterior measurements (Supplementary Table 1) as the circumference for top and bottom of the cone. I then determined the trapezoidal area of each organ by using the posterior and anterior circumference as the upper and lower bases and the length as the height of the trapezoid. I did this for each absorptive organ.

Figure 4. Photograph of the posterior (left) and anterior (right) view of the liver of *Procyon lotor* specimen UME5. This liver is the most representative of the specimens studied by qualitative appearance.

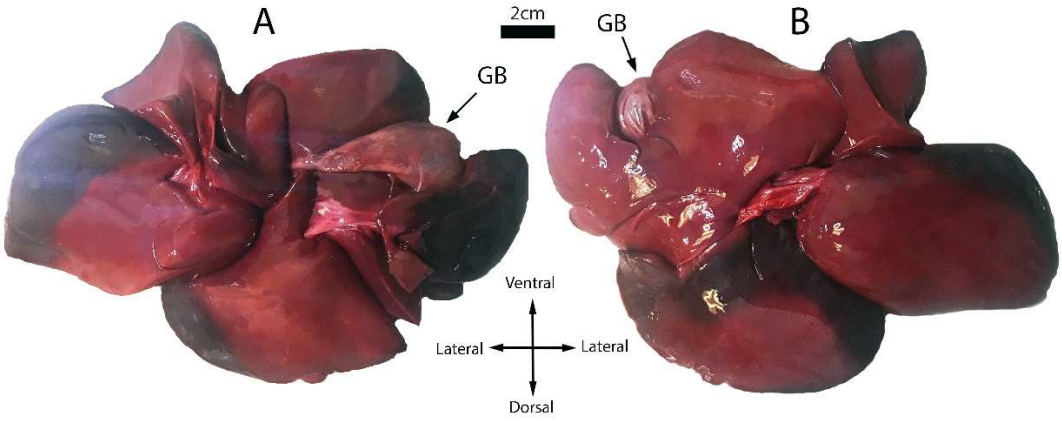


Figure 5. Photographs of the stomach of *Procyon lotor*. A, intact stomach with arrows pointing to the sphincters; B, the same stomach, butterflied, emptied of contents and washed; arrows pointing to the sphincters. 1 indicates the cardiac sphincter; 2 indicates the pyloric sphincter.

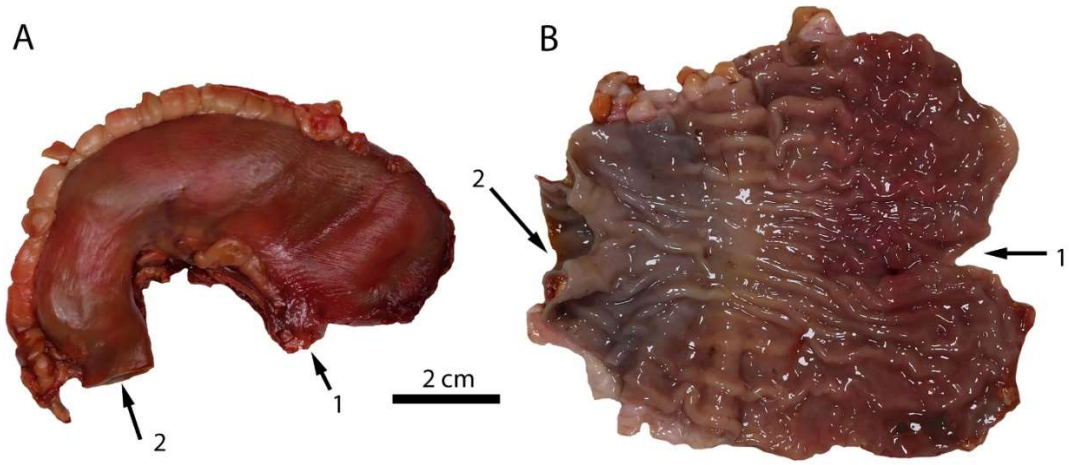


Table 3. Measurements of length of the hollow organs normalized by skull length (organ length/skull length). Abbreviations: **GI**, gastrointestinal; **SI**, small intestine; **LI**, large intestine.

Specimen	Total GI	Esophagus	Stomach	SI	LI
RMH1	42.4	1.7	1.3	35.8	4.1
RMH2	47.7	1.8	0.9	42.2	2.7
RMS3	39.6	1.7	1.7	33.6	3.1
UFE1	51.3	2.0	1.7	44.8	2.6
UFE2	41.3	1.8	1.0	37.5	3.1
UME3	41.4	1.7	1.4	39.7	3.0
UFE4	40.3	1.9	1.1	23.5	2.4
UME5	57.1	2.0	1.5	54.2	3.3

The dental measurements were converted to ratios to normalize them for body size differences (Table 5). They were then input into a Principal Component Analysis (PCA) following Calede et al. (2018) (Fig. 6). Because of the currently low sample size of rural raccoons, I was unable to run statistical analyses to explore differences between the two ecologies in individual measurements of the digestive system. Instead, I adopted a multivariate statistics approach and used an ordination method (PCA) to assess potential clustering of ecologies in a morphological space built from the measurements of the raccoons' gastro-intestinal tract and accessory organs (Fig. 7). All PCAs were run in R 3.5.3 (R Development Core Team, 2015) using RStudio 1.1.463 (RStudio, 2015), the package vegan 2.5-4 (Oksanen et al., 2015), and biostats (McGarigal, 2015).

Table 4. Measurements of mass of organs normalized by body mass (mass of organ/body mass). Abbreviations: **G.O.**, Greater omentum.

Specimen	G.O.	Whole GI	Liver	Pancreas	Stomach
RMH1	0.02	0.04	0.02	0.00	0.01
RMH2	0.03	0.04	0.02	0.00	0.00
RMS3	0.01	0.03	0.03	0.01	0.01
UFE1	0.02	0.03	0.02	0.00	0.00
UFE2	0.02	0.03	0.02	0.00	0.00
UME3	0.01	0.05	0.02	0.00	0.01
UFE4	0.02	0.05	0.03	0.00	0.01
UME5	0.01	0.05	0.04	0.01	0.01

Table 5. Measurement ratios of the upper teeth, P4 and M1, of the specimens studied. Abbreviations: **CL**, canine length; **P4LB**, length of P4; **P4W**, width of P4; **P4PM**, length of basin on P4; **PRBL**, length of shearing blade on P4; **M1BL**, length of shearing surface on M1; **M1LL**, length of M1; **M1W**, width of M1.

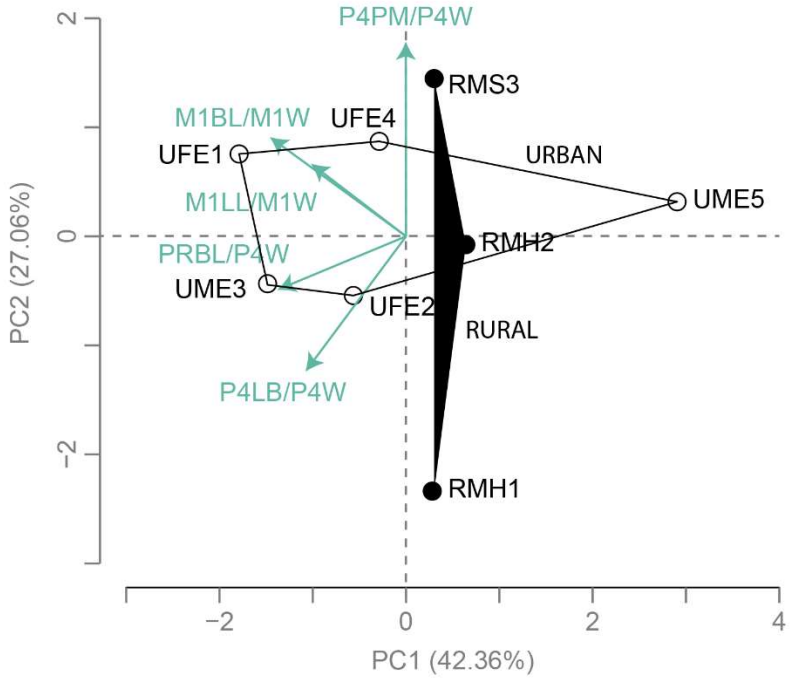
Specimen	P4LB/P4W	P4PM/P4W	PRBL/P4W	M1BL/M1W	M1LL/M1W	CL
RMH1	1.12	0.35	0.92	1.00	0.72	11.40
RMH2	1.06	0.48	0.91	1.00	0.72	13.76
RMS3	0.98	0.47	0.73	1.08	0.85	11.65
UFE1	1.13	0.49	0.94	1.11	0.89	10.44
UFE2	1.07	0.38	0.80	1.05	0.91	NA
UME3	1.18	0.45	0.88	1.08	0.85	10.58
UFE4	1.01	0.47	0.93	1.11	0.75	10.71
UME5	1.01	0.46	0.47	0.94	0.75	13.20

RESULTS

Dentition

There is no clustering of the urban and rural individuals in my analysis of tooth shape (Fig. 1); P4 and M1 do not differ in proportions between the two ecologies. Most specimens display similar degrees of development of blades and crushing surfaces in both P4 and M1 (especially M1BL, M1LL, PRBL), a result consistent with raccoons included in Calede et. al. (2018). Although there are no significant differences between ecologies, an interesting pattern emerges in which the variation among urban individuals is concentrated along PC1 and the degree of elongation of the blades of P4 and M1 (Fig. 1), as well as the relative size of the crushing surface on M1 whereas the variation among rural individuals is concentrated along PC2 and the change in relative length of the crushing basin of P4.

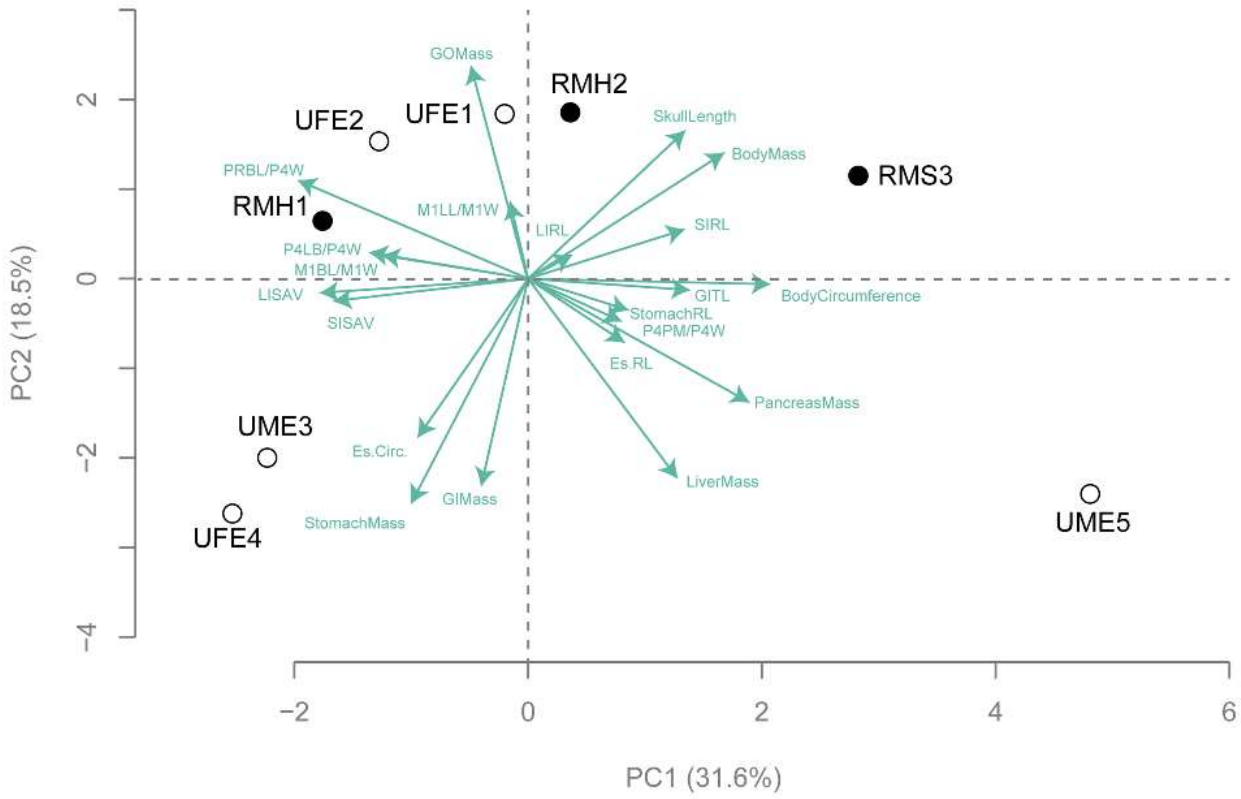
Figure 6. Principal component analysis of dental variables. Teal arrows indicate eigenvectors. Rural specimens are labeled by filled black circles, urban specimens are labeled by unfilled black circles. Abbreviations: **P4LB/P4W**, length of P4 over width of P4; **P4PM/P4W**, length of the P4 basin over P4 width; **PRBL/P4W**, length of shearing blade on P4 over P4 width; **M1BL/M1W**, length of shearing surface of M1 over M1 width; **M1LL/M1W**, length of M1 over M1 width.



Peritoneal cavity and greater omentum

The qualitative observation of the organs upon opening of the peritoneal cavity was little informative with regards to differences between rural and urban raccoons. The size of the organs, the adipose content, as well as the texture and turgor of the tissues varied greatly between individuals, even within ecological categories. A primary driver of this variation appears to be the result of feeding. Indeed, several individuals (RMS3, UFE1 and UME3) had eaten recently before death; all had gorged themselves. As a consequence, they had a stomach and intestine surface areas simple to three times large than their non-feeding counterparts (Supplementary Table 1). They also had stomachs with a smooth lining lacking obvious rugae because of stretching. Overall gut length and mass were not defining factors in ecology evident in the PCA of all components (Fig. 7).

Figure 7. Principal component analysis of all variables measured in this study. Teal arrows indicate eigenvectors. Rural specimens are labeled by filled black circles, urban specimens are labeled by unfilled black circles. Abbreviations: **GOMass**, normalized mass of the greater omentum; **SkullLength**, length of the skull; **BodyMass**, body mass of the specimen; **SIRL**, the normalized length of the small intestine; **BodyCircumference**, circumference of the specimen taken at the widest point of the abdomen; **GITL**, gastrointestinal total length; **StomachRL**, normalized length of the stomach; **EsophagusRL**, normalized length of the esophagus; **PancreasMass**, normalized mass of the pancreas; **LiverMass**, normalized mass of the liver; **GIMass**, normalized mass of the gastrointestinal tract, **StomachMass**, normalized mass of the stomach, **Es.Circ**, normalized, mean circumference of the esophagus; **SISAV**, surface area to volume ratio of the small intestine; **LISAV**, surface area to volume ratio of the large intestine; **P4LB/P4W**, length of P4 over width of P4; **P4PM/P4W**, length of the P4 basin over P4 width; **PRBL/P4W**, length of shearing blade on P4 over P4 width; **M1BL/M1W**, length of shearing surface of M1 over M1 width; **M1LL/M1W**,length of M1 over M1 width



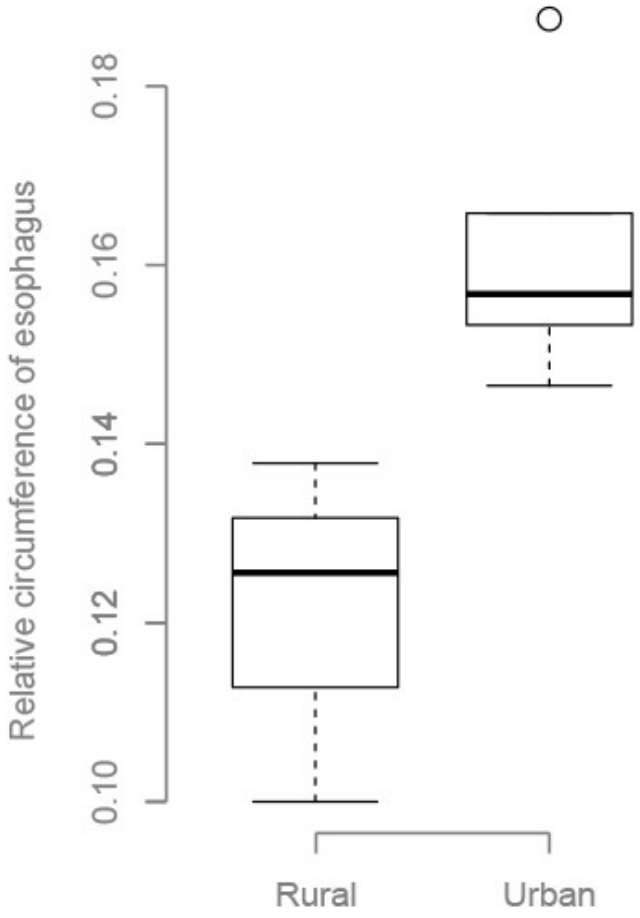
Although the size of the greater omentum varied among individuals, the mesentery was similar in anatomy across individuals studied. In all individuals, the greater omentum consists of two peritoneal sheets. Each sheet displayed similar vascularity and adipose content between individuals. The greater omentum wrapped around the whole gut tube (Fig. 2) and either did not connect to the posterior and dorsal aspects of the peritoneum or was loosely connected so as to

offer no resistance in removal. The omentum spans the entire surface of the peritoneum. Males carried the omentum towards the upper half of the abdomen while females carried it in the lower half of the abdomen or evenly throughout (Fig. 2). The lesser omentum, weighing about two to three grams, connected the intestines to the dorsal wall of the abdomen. The mass of the greater omentum ranged greatly among individuals (Table 4) but did not differ significantly between the two ecologies.

Esophagus

The esophagus runs from the glottis to the cardiac sphincter of the stomach and follows the trachea and aorta to the stomach. It is thinly muscular and exhibits more flexibility than the other organs of the gut tract. The esophagus has visible striations running anterior to posterior. It demonstrates the least amount of variation in length and circumference among individuals of any organ studied (Supplementary Table 1). The relative circumference of the esophagus is the only variable measured for which there is no overlap between rural and urban raccoons, The length and surface area of the esophagus do not differ between categories.

Figure 8. Measurements of normalized esophagus circumference (mean esophagus circumference/skull length) comparing rural and urban ecologies.



Stomach

A unilocular organ attaching at the posterior end of the esophagus and the anterior end of the duodenum, the stomach is slightly curved with a fundus, body, and pylorus. The exterior is smooth and the greater curvature attaches to the greater omentum. The thick tissue is very elastic. The smallest stomach length ratio was 0.845 and the largest was 1.72. Rugae were present in five of the eight specimens studied; those that had not recently fed and therefore

stretched their stomach. The length and width of the stomach varied greatly among individuals; there is no consistent difference between the two ecologies. The surface area of the stomach was also not significantly different between categories. The size of the stomach is not an important variable in the PCA (Fig. 7).

Small intestine

The three segments of the small intestine, including duodenum, jejunum and ileum, cannot be differentiated using only gross anatomy; I therefore only consider the small intestine, from the pylorus to the ileocolic junction, as a whole hereafter. The small intestine varies in length between individuals, however there is no clear pattern of variation between rural and urban populations. The surface area of the small intestine had the most variability of all organs studied (Table 3). Intestinal wall thickness and circumference differ among individuals but not between ecologies (Supplementary Table 1). There is also no apparent pattern of differences between ecological categories in surface area to volume ratio (SAV) between urban and rural raccoons (Fig.7).

Table 6. Measurements of surface area to volume ratio, esophagus circumference ratio. Esophagus circumference ratio is the ratio of average esophagus circumference normalized by skull length (mean esophagus circumference/skull length). The small intestine and the large intestine surface area to volume ratio is comparing the surface area of the organ with the volume of the same organ (organ surface area/organ volume). Abbreviations: **G.O.**, greater omentum; **LI**, large intestine; **SI**, small intestine**; SAV**, surface area to volume ratio.

Specimen	Esophagus circumference ratio	SI SAV ratio	LI SAV ratio
RMH1	0.23	0.12	0.07
RMH2	0.23	0.10	0.06
RMS3	0.22	0.06	0.04
UFE1	0.31	0.08	0.06
UFE2	0.28	0.12	0.05
UME3	0.37	0.08	0.05
UFE4	0.32	0.16	0.07
UME5	0.29	0.07	0.05

Colon

The colon is a simple tube comprising a slight transverse colon, a descending colon, and a rectum; there is no cecum or ascending colon present. The colon directly attaches to the posterior end of the ileum and ends at the anus. The colon is larger in circumference than the ileum. The PCA indicates that there is no relationship between ecology and colon SAV or colon length (Fig. 7).

Liver

The liver includes six lobes connected by a fusiform ligament (Fig. 4). The lobes range in color, shape, and size. The liver to body mass ratios varies from simple to double (Table 4). The liver rests atop the stomach's fundus and the most posterior lobe conforms to the shape of the fundus. In the individuals collected, the liver turgor varied from soft and malleable to firm and inflexible. Three individuals, two rural and one urban, showed color, turgor, and surface conditions consistent with a fatty liver. There is no apparent association between liver mass and ecology.

Pancreas

The pancreas consists of a dorsal and a ventral lobe connected to the duodenum through connective tissue for one to two centimeters along the intestinal surface. The size of the pancreas ranged from simple to double across individuals but does not differ between ecologies (Supplementary Table 1).

DISCUSSION

This study is the first formal documentation of the entire digestive system of the raccoon. Such work is critical to the necropsies of raccoons and the study of this common North American mammal commensal with humans.

There is little evidence that the alimentary canal of raccoons differs between rural and urban populations in central Ohio. The results of my analyses do not support an increased ability to feed on anthropogenic foods in urban raccoons relative to rural ones. Indeed, the results of the principal component analyses (Fig. 7) show no particular clustering of the two populations of raccoons.

Although there is no clustering of the urban and rural populations in my analysis of tooth shape, the distribution of individuals in the PCA is noteworthy. Rural raccoons appear to vary little in their anatomical correlates of carnivory (Popowics, 2003; Calede et al. 2018), displaying intermediate values of blade length, but vary greatly in the length of the crushing basin on P4, a correlate of omnivory (Calede et al. 2018). The opposite is true of urban animals, which also mostly display greater blade lengths than rural individuals (with the exception of one raccoon, (Fig. 6). Should this pattern be confirmed by the addition of more individuals in the analysis, this may suggest a greater range of shearing capabilities in urban animals than in rural ones.

The primary function of the esophagus is to transport the bolus from the mouth to the stomach (Kardong et al., 2012). I focused my analyses on correlates of transport, the length and relative circumference. The esophagus of a raccoon is very flexible and can accommodate a large bolus.

A narrowed esophagus could negatively affect the raccoon's ability to feed whereas an expanded esophagus might enable the accommodation of larger amounts of food per bite. I did observe a greater relative circumference of the esophagus in urban raccoons than in their urban counterparts (Fig. 8). This may be indicative of enhanced gorging capability in urban animals associated to feeding in an environment with heightened competition with conspecifics and increased risk of confrontation with humans. Such conclusion awaits a formal statistical test requiring a greater sample size.

The surface area of the stomach was widely distributed in both categories of animals. This is likely a consequence of the length of fasting prior to death and the associated distension of the stomach, or lack thereof. The other measurements of the stomach are also dependent on the timing of their last intake of food prior to death. It is possible that the stomach will be little informative regarding anatomical adaptations or acclimations to an urban diet at the scale of gross anatomy. I discuss below some possible insights we may gain from microscopic anatomy.

There is no difference between the two categories of animals with regards to the length and surface area to volume ratios of the whole GI tract, small intestine and large intestine. The absence of differences in the anatomy of the intestine implies a lack of differences in absorption between the two populations. This may not be a completely unexpected result, but I am skeptical that gross morphology is sufficient to assess the surface area to volume ratio of the intestine, the critical variable reflecting the absorption capabilities of the intestine. I propose below the addition of a histological analysis.

I expected a greater liver mass, pancreas mass, and gallbladder volume associated to more intense processing of fats in urban raccoons exposed to a fat-rich diet from anthropogenic foods as opposed to a leaner diet in rural animals. However, I found no differences in accessory digestive organs between the two ecologies. The volume to body mass ratio of the gallbladder is similar across both categories of raccoons and there are no differences in the relative mass of the liver either. Remarkably, I could not identify a gallbladder in one of the rural individuals. A greater number of individuals will be necessary to assess the uniqueness of such feature.

Although there is no apparent differences in digestive system anatomy between rural and urban raccoons, a larger number of individuals dissected may be necessary to detect subtle differences in anatomy, especially in light of an overlap between the two ecological categories. Thus, it may be possible that additional sampling will reveal that urban animals cluster around lower PC2 scores (Fig. 7) characterized by higher liver mass, higher pancreas mass, lower greater omentum mass, and greater esophagus circumference. These characteristics would be consistent with my predictions of increased capacity to process fats and sugars in urban raccoons, an increased ability to gorge, and less reliance on energy storage.

This research has shown promise in investigating the impacts of human encroachment on wildlife. Such analyses may reveal the ecological and evolutionary impacts of urbanization and inform responsible decision making by policy makers and wildlife advocacy groups. It may also be a springboard to investigate potential ramifications for human health. Indeed, raccoons proximity to urban centers makes them prime contributors in zoonoses infections involving raccoon roundworms (*Baylisascaris procyonis*) (Sato & Suzuki, 2006).

I am planning future analyses including more individuals along with histology and DNA analyses. Additional specimens are necessary to confirm the patterns uncovered by the work described herein. A histological analysis would enable an assessment of the microscopic anatomy of the liver and small intestine, among other organs. I would specifically test for the difference in glycogen content within the liver between the two populations as well as differences in absorption capabilities (based on the morphology of the intestinal villi) of the small intestine. Within the stomach, I would evaluate the fundic glands and compare proportions across ecologies. A histological approach would also help test for specific pathologies. Thus, two urban raccoons exhibited liver surface conditions consistent with fatty liver disease: lighter surface pigment, a yellow interior, and a webbed pattern across the liver surface. A DNA analysis would enable an estimation of the genetic isolation between the two racoon populations and inform the potential for adaptation.

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Appendix

Supplementary Table 1: Measurements of the digestive system of the raccoons studied.

Measurement:	RMH1	RMH2	RMS3	UFE1	UFE2	UME3	UFE4	UME5
Total Mass (g)	4,600	5,700	7,100	6,100	5,300	2,900	4,500	6,400
Skull Length in (cm)	11.1	10.9	12.0	10.479	10.5	10.0	9.8	10.7
SVL (cm)	58.2	57.8	65.5	62.1	59.5	51.1	53.4	56.5
Body Circ (cm)	37.5	43.2	50.0	42.5	39.7	40.9	39.9	48.2
C1U length (mm)	11.4	13.6	11.7	10.4	NA	10.6	10.7	13.2
C1L Length (mm)	12.7	11.1	11.6	10.2	NA	11.1	8.7	13.6
P4LB (mm)	7.78	8.03	8.47	8.72	8.19	8.42	7.38	8.30
P4W (mm)	6.93	7.51	8.69	7.75	7.69	7.15	7.28	8.22
P4PM (mm)	2.44	3.61	4.04	3.83	2.89	3.18	3.44	3.80
PRBL (mm)	6.34	6.80	6.31	7.31	6.16	6.32	6.78	3.85
M1BL (mm)	7.99	8.62	9.38	9.70	8.48	9.31	9.85	8.98
M1LL (mm)	5.76	6.19	7.34	7.76	7.35	7.38	6.63	7.20
M1W (mm)	8.01	8.59	8.66	8.77	8.11	8.65	8.90	9.55
G.O. Weight (g)	79	180	97	132	129	23	66	56
G.O. Weight Ratio	0.02	0.03	0.01	0.02	0.02	0.01	0.02	0.01
GB Volume (ml)	4.58	5.20	0.00	5.75	4.70	3.50	5.10	6.80
GB Volume Ratio ($*10^{-4}$ ml/g)	9.96	9.12	NA	9.42	8.87	12.10	11.0	11.0
Pancreas Weight (g)	14	21	32	16	17	9	17	39
Pancreas Weight Ratio	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.01
Liver Weight (g)	113	125	183	114	115	68	134	250
Liver Weight Ratio	0.02	0.02	0.03	0.02	0.02	0.02	0.03	0.04
GI Length (cm)	471	519	475	539	432	412.5	395	611
GI Weight (g)	194	248	238	198	176	136	222	291
GI Surface Area (cm^3)	1,366.9	1,650.9	2,416.1	2,249.6	1,553.4	1,930.4	693.7	3,002.7
GI Weight Ratio	0.04	0.04	0.03	0.03	0.03	0.05	0.05	0.05
GI Length Ratio	42.4	47.7	39.6	51.3	41.3	41.4	40.3	57.1
Esophagus Length (cm)	18.5	19.5	20.7	21.2	18.5	16.8	19.0	21.5
Esophagus Ant Circ (cm)	2.4	2.0	2.2	3.0	2.8	2.9	3.1	3.2
Esophagus Pos Circ (cm)	2.7	1.9	3.0	3.5	3.0	3.4	3.2	3.1
Esophagus Weight (g)	6	3	6	5	7	4	7	9
Esophagus SA (cm^3)	47.2	38.0	52.3	68.9	53.7	52.9	59.9	67.7
Esophagus Weight Ratio	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Esophagus Length Ratio	1.7	1.8	1.7	2.0	1.8	1.7	1.9	2.0
Stomach Length (cm)	14.0	9.2	20.5	18.0	10.2	13.8	11.0	15.5
Stomach Width (cm)	3.1	3.6	9.9	8.2	4.1	7.7	4.0	6.1
Stomach Weight (g)	21	20	32	25	23	19	30	30
Stomach Weight Ratio	0.00	0.00	0.01	0.00	0.00	0.01	0.01	0.01

Stomach Length Ratio	1.1	0.9	1.7	1.7	1.0	1.4	1.1	1.5
Stomach SA (cm^2)	61.8	49.2	227.2	128.0	63.0	112.0	62.6	78.2
SI Length (cm)	398.1	459.0	402.2	469.9	394.0	396.0	230.5	580.0
SI Ant Circ (cm)	3.1	3.7	4.1	4.6	2.6	3.9	1.5	5.8
SI Pos Circ (cm)	2.1	2.4	5.5	3.5	2.7	4.1	2.5	3.2
SI Weight (g)	145	208	158	144	127	103	157	227
SI SA (cm^2)	1,035.1	1,400.0	1,850.1	1,903.1	1,044.1	1,584.0	461.0	2,610.0
SI Weight Ratio	0.03	0.04	0.02	0.02	0.02	0.04	0.04	0.04
SI Length Ratio	35.8	42.2	33.6	44.8	37.5	39.7	23.5	54.2
Conical Volume (cm^3)	8,559	13,617	29,318	24,363	8,693	19,909	2,957	37,924
SAV Ratio (cm^-1)	0.12	0.10	0.06	0.08	0.12	0.08	0.16	0.07
LI Length (cm)	45.5	29.5	36.5	27.2	33.0	30.0	23.2	35.5
LI Ant Circ (cm)	4.5	3.9	8.1	5.8	4.8	5.4	3.5	6.7
LI Pos Circ (cm)	5.3	7.2	7.6	5.2	7.1	6.7	6.0	7.2
LI Weight (g)	21	16	32	22	19	14	31	27
LI SA (cm^2)	223.0	163.7	286.5	149.6	196.4	181.5	110.2	246.7
LI Weight Ratio	0.01	0.00	0.01	0.00	0.00	0.01	0.01	0.00
LI Length Ratio	4.1	2.7	3.1	2.6	3.1	3.0	2.4	3.3
Conical Volume (cm^3)	3,439	2,938	7,068	2,587	3,715	3,463	1,682	5,389
SAV Ratio (cm^-1)	0.07	0.06	0.04	0.06	0.05	0.05	0.07	0.05
Conical volume (cm^3)	25,145	47,150	48,572	37,542	33,818	38,467	12,553	82,012

Supplementary Table 2: Principal component scores for the dental morphology analysis.

	RMH1	RMH2	RMS3	UFE1	UFE2	UME3	UFE4	UME5
PC1	0.280798	0.640321	0.301028	-1.789746	-0.564748	-1.484704	-0.287621	2.904672
PC2	-2.336581	-0.076670	1.446732	0.755478	-0.542812	-0.434183	0.870920	0.317116
PC3	-0.416139	-1.324837	0.495035	0.036036	1.509785	0.298057	-1.225648	0.627712
PC4	0.469479	-0.438682	0.730716	-0.695032	0.658149	-0.872465	0.835733	-0.687898
PC5	0.110090	-0.454313	-0.016714	-0.081110	-0.261523	0.275371	0.270265	0.157933

Supplementary Table 3: Eigenvectors for the dental morphology analysis.

	PC1	PC2	PC3	PC4	PC5
P4LB.P4W	-0.431557	-0.496333	0.035930	-0.700357	0.274992
P4PM.P4W	-0.001152	0.714914	-0.370608	-0.577571	-0.134011
PRBL.P4W	-0.552561	-0.196468	-0.522420	0.226772	-0.575958
M1BL.M1W	-0.584800	0.364333	-0.065366	0.347258	0.632779
M1LL.M1W	-0.407974	0.266858	0.764306	-0.062435	-0.417472

Supplementary Table 4**:** Principal component scores for overall analysis of all specimens studied.

	PC1	PC2	PC3	PC4	PC5	PC6	PC7
RMH1	-1.758103	0.645039	2.526738	-2.067517	0.077360	-0.261276	1.277538
RMH2	0.361242	1.855960	2.136767	1.844791	-0.527822	1.520534	-0.593472
RMS3	2.825116	1.149599	-1.489907	-0.522153	2.830717	0.425554	0.253062
UFE1	-0.200263	1.839456	-2.640654	0.984989	-1.944426	-0.343734	0.897979
UFE2	-1.275405	1.533110	0.093007	-0.643575	0.181386	-1.624730	-1.463030
UME3	-2.231758	-1.998933	-1.604337	-1.930186	-0.592388	1.356369	-0.605134
UFE4	-2.529543	-2.621674	0.111188	2.586353	1.230696	-0.522410	0.328667
UME5	4.808714	-2.402559	0.867196	-0.252700	-1.255523	-0.550307	-0.095609

Supplementary Table 5: Eigenvectors for overall analysis of all specimens studied.

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8
BodyMass	0.281324	0.235579	0.016594	0.198918	0.097165	-0.281928	0.175800	-0.308556
SkullLength	0.225394	0.277130	0.078776	-0.159495	0.289746	0.115365	0.276369	-0.161225
BodyCirc	0.346605	-0.010324	-0.156375	0.064927	0.141759	0.198267	-0.075748	0.006974
P4LB.P4W	-0.227898	0.049140	-0.081741	-0.255774	-0.412080	0.217270	0.049992	-0.284443
P4PM.P4W	0.134634	-0.080233	-0.256336	0.394795	-0.071292	0.401609	0.032028	-0.011024
PRBL.P4W	-0.329689	0.183851	-0.053394	0.106945	0.041897	0.219828	0.202534	0.000133
M1BL.M1W	-0.210117	0.043902	-0.399899	0.148554	0.197374	0.001407	0.100883	0.451997
M1LL.M1W	-0.026110	0.145773	-0.442893	-0.145317	-0.011568	-0.252416	-0.396470	-0.335754
GITL	0.232127	-0.021196	0.042477	0.113619	-0.509587	-0.039907	0.125112	-0.290505
EsophagusRL	0.139053	-0.120039	-0.140511	0.383280	-0.286400	-0.336445	0.171530	0.285368
StomachRL	0.144920	-0.059174	-0.365158	-0.185685	0.013168	-0.028824	0.616786	-0.027620
SIRL	0.224771	0.092267	0.000060	-0.179599	-0.474150	0.104719	-0.166299	0.371761
LIRL	0.064121	0.045294	0.250299	-0.498183	-0.002412	-0.138979	0.195827	0.316115
EsophagusCirc	-0.158327	-0.297179	-0.275381	-0.172944	-0.105988	-0.323945	-0.057895	0.036896
SISAV	-0.279174	-0.041913	0.265220	0.196248	0.078713	-0.309855	-0.030396	-0.039544
LISAV	-0.298418	-0.026539	0.184804	0.158793	-0.187223	-0.128053	0.379267	-0.115911
GOMass	-0.081989	0.403525	0.150059	0.274204	-0.055660	-0.056689	-0.136831	0.067498
GIMass	-0.067149	-0.387523	0.246226	0.075129	-0.038372	0.375223	0.004692	-0.023687
LiverMass	0.213890	-0.373035	0.150986	0.038614	0.098448	-0.188863	0.033986	-0.044011
PancreasMass	0.316808	-0.231004	0.130518	0.047068	0.120677	-0.050249	-0.124351	0.021774
StomachMass	-0.167539	-0.420165	-0.130033	-0.044283	0.150881	0.043749	0.008947	-0.228199

Abbreviations

SVL, Surface area to volume ratio; **Circ**, Circumference; **C1U**, first upper canine; **4LB**, length of P4; **P4W**, width of P4; **P4PM**, length of basin on P4; **PRBL**, length of shearing blade on P4; **M1BL**, length of shearing surface on M1; **M1LL**, length of M1; **M1W**, width of M1; **G.O.**, greater omentum; **GB**, gallbladder; **SA**, surface area; **GI**, gastrointestinal; **Ant**, anterior; **Pos**, posterior; **SI**, small intestine; **LI**, large intestine; : **GOMass**, normalized mass of the greater omentum; **SkullLength**, length of the skull; **BodyMass**, body mass of the specimen; **SIRL**, the normalized length of the small intestine; **BodyCircumference**, circumference of the specimen taken at the widest point of the abdomen; **GITL**, gastrointestinal total length; **StomachRL**, normalized length of the stomach; **EsophagusRL**, normalized length of the esophagus; **PancreasMass**, normalized mass of the pancreas; **LiverMass**, normalized mass of the liver; **GIMass**, normalized mass of the gastrointestinal tract, **StomachMass**, normalized mass of the stomach, **Es.Circ**, normalized, mean circumference of the esophagus; **SISAV**, surface area to volume ratio of the small intestine; **LISAV**, surface area to volume ratio of the large intestine; **P4LB/P4W**, length of P4 over width of P4; **P4PM/P4W**, length of the P4 basin over P4 width; **PRBL/P4W**, length of shearing blade on P4 over P4 width; **M1BL/M1W**, length of shearing surface of M1 over M1 width; **M1LL/M1W**,length of M1 over M1 width.